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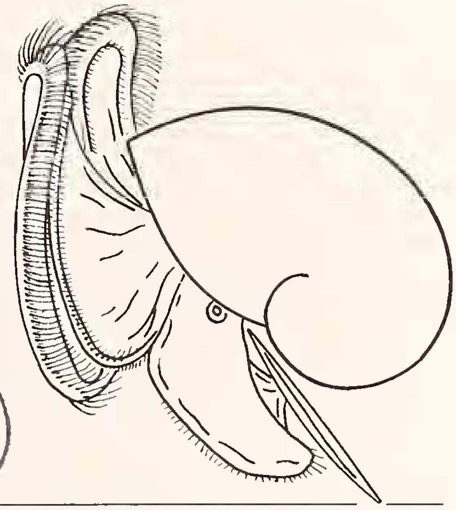

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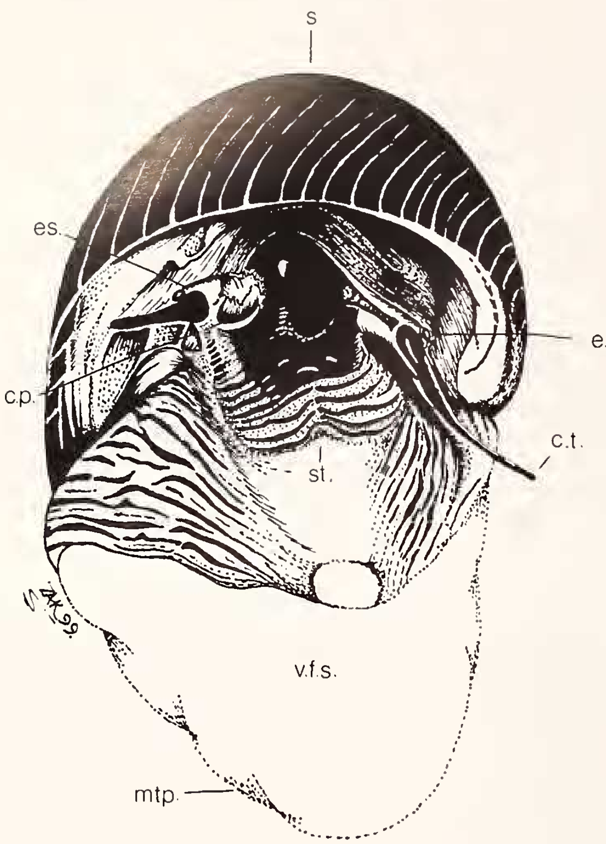

Figure 1

Ink illustration of *Nerita picea*. Key: c.p., cephallic penis; c.t., cephalic tentacle; e., eye; es., eye-stalk; mtp., metapodium; s., shell, st., snout; v.f.s., ventral foot sole. Drawing by C. Z. Womersley from a photograph by L. M. Gutiérrez.

these. The coloration of the animals is pale gray, with black pigmentation on the upper surface of the snout, the sides of the foot, the mantle edge, and in males, the cephalic penis. This pigmentation occurs in highly concentrated flecks that form horizontal black bands, or "tiger striping" (Figure 1). The cephalic tentacles carry long longitudinal black lines on the upper surface, but these fade toward the underside. The apical regions of the eye-stalk have a high concentration of pigmentation, which is not set in any distinct pattern. The sole of the foot is unpigmented. The snail carries the operculum on the posterior foot lobe (metapodium). When crawling, *N. picea* exposes part of its snout, both cephalic tentacles, and the eyes (not eye-stalks) at the edge of the shell.

Specimens of adult *N. picea* (n = 4264) were collected during morning low tides from two intertidal rocky shores, Sandy Beach and Pupukea, located on opposite sides on the island of O'ahu. The two sites were chosen to allow comparison of shadow responses by two different populations of snails from different substrates and exposure. Sandy Beach is primarily composed of black volcanic boulders that are highly exposed to surf action. Conversely, Pupukea is mainly a limestone rocky shore with volcanic boulders dispersed throughout and is more sheltered from the effects of surf action due to the presence of a limestone bench offshore. The geomorphology of these two beaches has been discussed elsewhere (Wentworth, 1938, 1939). Snails were maintained in glass aquaria with running seawater and provided with a 12light:12dark cycle. Mean shell measurements for Sandy Beach and Pupukea snails were 12.11 mm (length), 9.7 mm (width), 6.57 mm (height); and 15.77 mm (length), 10.478 mm (width), and 7.457 mm (height), respectively. Individual sets of snails collected from both these sites were subjected to two series of experiments described below.

Shadow Response of Normal Snails

Three tests were devised to determine the shadow responses of various parts of the body: (1) "Crawling." In this position, snails exposed part of the snout, both cephalic tentacles, and the eyes at the edge of the shell, in addition to the anterior and lateral portions of the foot, i.e., maximal pigmentation exposure; (2) "Sole of Foot." Snails were turned upside down and allowed to emerge from the shell until the sole of the foot was maximally extended. In this position, the foot almost covered the entire shell, and no anterior, lateral, or posterior foot lobes were visible, i.e., minimal or no pigmentation exposure; (3) "Metapodium." Snails were turned upside down and allowed to retreat into their shells. Testing occurred when the snail emerged from the shell at a point when only the metapodium, to which the operculum is attached and carried, was visible, i.e., partial pigmentation exposure.

Representative individuals of both snail populations were placed in one of the above test positions and exposed to a shadow stimulus by passing a square black card (8 × 8 cm) through a light source, decreasing the illumination from an initial light level of 1.1–1400 to 0 lux. The stimulus period lasted approximately 1 second. A light source (100 watts) was located 0.75 m above the experimental animals inside a completely enclosed 2 × 1 × 1 m matte black box ensuring uniform illumination. Temperature effects of the light source on experimental subjects were nil. Light intensities, representing a gradation from full moon (1.1 lux) to dusk or dawn (1400 lux), were controlled via a previously calibrated dimmer and measured with a GE light meter (Model No. 27A). Shadow responses of individual snails were observed at six different light intensities (1.1, 110, 320, 540, 750, and 1400 lux). All experiments were conducted in a dark room at night to avoid interference from ambient light, and the observer wore black to negate reflection from clothing.

A snail's reaction to a passing shadow was scored as either "response" or "no response." A simultaneous contraction of both tentacles and/or snails retreating into the shell constituted a positive response. All other behaviors were scored as "no response." Because of the rapid habituation of snails to sequentially repeated shadow stimuli (LMG, unpublished observations), individual snails were only tested once.

Shadow Response of Blinded and Ablated Snails

To discern whether the eyes or cephalic tentacles mediated shadow responses, snails of both populations were anesthetized for 15 min in 7.5% $MgCl_2$ and either (1) the cephalic tentacles or (2) the eyes and the eye-stalks removed with iridectomy dissecting micro-scissors. Surgically treated animals were allowed to recover for 24–48 hr before being exposed to shadow stimuli in one of the three test positions in an identical manner to that described for normal snails. Control experiments used snails previously anesthetized that had an incision in the basal area of the eye and tentacles.

Statistical Analysis

Chi-square tests were conducted to assess the significance of the difference in shadow responses by snails exposed to shadow stimuli in each of the three test positions. Shadow responses with probabilities less than 0.05 indicated that a response was dependent on the body area being tested.

RESULTS

Nerita picea displayed two common responses to passing shadows. First, when crawling, there was either (a) a simultaneous contraction of both cephalic tentacles, or (b) contraction of cephalic tentacles coupled with a partial to full retreat of the snout or whole body into the shell. Second, when turned upside down, snails only exhibited a partial or full retreat into the shell; cephalic tentacles were retracted in the shell in blind and normal snails. Interestingly, as snails turned over and made contact with the substratum, shadow stimulation did not arouse a withdrawal response, and turning continued until the snail was in the upright position. Type of habitat, volcanic versus limestone, did not affect the shadow responses of snails (Table 1), as shadow responses did not vary between snail populations from Pupukea or Sandy Beach. Thus, the data presented represents a pooling of both populations.

Shadow Response of Normal Snails

Nerita picea demonstrated withdrawal responses to a passing shadow, and both body position and light intensity affected the intensity of response (Figure 2a, Table 2). "Crawling" and "metapodium" snails exhibited a positive dependence on light intensity with respect to the number of shadow responses (Crawling, χ^2: 64.75, n = 396, $P < 0.001$; Metapodium, χ^2: 72.467, n = 396, $P < 0.001$) (Figure 2a). At low light intensities (1.1–540 lux), "metapodium" snails showed reduced responses compared to "crawling" snails, but at higher light levels (750 and 1400 lux), showed a similar number of responses (Figure 2a, Table 2). Conversely, the responses of "sole of foot" snails were highly reduced at all light intensities and therefore not dependent on light intensity (χ^2: 10.923, n = 396, $P > 0.05$) (Figure 2a).

Table 1

Chi-Square test results assessing whether degree of responses to shadow stimuli by *N. picea* is independent of beach of origin. Snails were collected from Sandy Beach and Pupukea.

Test position	$\chi^{2\,a}$ response	$\chi^{2\,a}$ no response	No. of trials	P^b
Crawling	0.566	4.812	198	NS[b]
Sole of Foot	10.857	3.325	198	NS[b]
Metapodium	1.823	0.184	198	NS[b]

[a] χ^2 (0.05, 10) = 11.07.
[b] NS = non significant differences, $P > 0.05$.

Shadow Responses of Blind and Ablated Snails

Both blind and ablated snails exhibited positive shadow responses that were dependent on light intensity in all three test positions (Figures 2b, c, Table 3).

Blinded Snails. Blind "crawling" snails exhibited more positive responses than blind "sole of foot" snails at all light intensities (Figure 2b). "Crawling" and "metapodium" snails showed similar responses at most light intensities, but at 110 and 540 lux, more "metapodium" snails failed to respond to a passing shadow. There was no significant difference ($P > 0.05$) between the negative shadow response of "sole of foot" and "metapodium" snails.

Ablated Tentacle Snails. Ablated "crawling" snails behaved similarly to "metapodium" snails at most light intensities (Figure 2c). More "sole of foot" snails failed to respond to a shadow than "crawling" or "metapodium" snails at most light intensities (320–1400 lux). At 110 lux, "metapodium" and "sole of foot" snails behaved similarly, showing more negative responses to shadow stimuli. Irrespective of test position, the majority of ablated tentacle snails failed to respond at low light levels (1.1. lux).

Comparison of responses between ablated/blind, normal/blind, and normal/ablated snails is presented in Table 4. With the exception of lower light intensities (1.1 and 320 lux) where more "crawling" blind snails showed positive responses to shadow (Table 4a), no differences were observed in the shadow responses of blind and ablated snails in the three test positions. Both normal and

Figure 2

Shadow responses of adult *Nerita picea*. a) normal snails, b) blind snails, and c) snails with ablated tentacles.

Table 2

Chi-Square test results for shadow responses of normal snails (pooled data) in "crawling," "sole of foot," and "metapodium" positions tested.

Light intensity (lux)	Crawling[a] vs. sole of foot		Crawling vs. metapodium[a]		Sole of foot[a] vs. metapodium	
	$\chi^{2\,c}$	*P*	$\chi^{2\,c}$	*P*	$\chi^{2\,c}$	*P*
1.1	26.16	< 0.001	6.896	< 0.05	7.1249	< 0.05
110	19.049	< 0.001	9.827	< 0.01	1.6901	NS[b]
320	45.819	< 0.001	21.286	< 0.001	6.0789	< 0.05
540	37.562	< 0.001	14.687	< 0.001	6.8575	< 0.05
750	54.559	< 0.001	4.552	NS[b]	33.625	< 0.001
1400	53.387	< 0.001	0.151	NS[b]	50.256	< 0.001

[a] N = 66 per light intensity.
[b] NS = non significant differences, P > 0.05.
[c] χ^2 (0.05, 2) = 5.991.

blind snails in either the "crawling" or "metapodium" position responded similarly to shadow at higher light intensities (Figures 2a, b, Table 4). At lower light intensities (110 lux), more "crawling" blind snails and less "metapodium" blind snails responded positively when compared to normal snails. In comparison to normal "sole of foot" snails, blind "sole of foot" snails showed more negative responses at most light intensities (320, 750, and 1400 lux). Shadow responses of blind "sole of foot" snails increased with increasing light intensity (Figure 2b). With the exception of low light levels (1.1 and 110 lux), shadow responses of normal and ablated snails in the "crawling" position were not significantly different (Table 4c). Unlike normal snails, more "metapodium" ablated snails failed to respond to a passing shadow at 110, 320, and 540 lux. The shadow responses of "metapodium" ablated snails increased with increasing light intensity (Figure 2c).

DISCUSSION

In the present study, *N. picea* from two different habitats (Sandy Beach and Pupukea) exhibited similar withdrawal responses to passing shadows. Shadow responses showed little impairment when differentiated eyes and eye-stalks or cephalic tentacles were removed, indicating that shadow responses in *N. picea* are mediated, in large part, by receptors other than the eyes. These results are entirely consistent with the observation that many molluscan responses to light are based on dermal receptors (Land, 1968). For example, the reactions of *N. reticulatus* to shadow were not affected by eye removal (Crisp, 1972), and shadow crossing the cephalic tentacles of *Helix* elicited no response, but the animal fully withdrew when shadow crossed the mantle near the base of the shell (Föh, 1932).

Table 3

Chi-Square test results assessing independence of shadow responses to light intensity of blind and ablated snails.

Test position	Blind snails[a]		Ablated snails[a]	
	$\chi^{2\,b}$	*P*	$\chi^{2\,b}$	*P*
Crawling	45.7233	< 0.001	130.08	< 0.001
Sole of foot	36.211	< 0.001	29.8331	< 0.001
Metapodium	41.6327	< 0.001	60.2459	< 0.001

[a] N = 198 per test position per experimental treatment.
[b] χ^2 (0.05, 5) = 11.070.

Snail posture studies (Figure 2) suggest that the dermal receptors involved are closely associated with the dark pigmentation, "tiger striping," of the foot (Figure 1). Consequently, snails in the "crawling" position which had more pigmented body areas exposed, i.e., snout, anterior, posterior, and lateral foot lobes, eyes and/or tentacles, if present, were generally more responsive to light irrespective of experimental treatment (Table 2). Conversely, the "metapodium" position, which only allowed snails to expose the highly pigmented posterior part of the metapodium, and "sole of foot" snails, which exposed only the unpigmented ventral foot surface, were less responsive to shadows. Thus, like the black garden slug *Arion ater,* in which the amount of porphyrin present (known to cause photosensitivity) is directly proportional to the amount of dark pigment in the integument (Kennedy, 1959), the amount of dermal pigmentation in *N. picea* would appear to be directly proportional to dermal photosensitivity. The importance of the dermal photosensory system of *N. picea* is emphasized by the fact that it allowed blind and ablated snails to keenly respond to shadow stimuli at very low light levels (1.1 lux), allowing them to conduct a correct defense response even in a dimly lit environment.

In conjunction with both ocular and dermal receptors, our results also suggest that the darkly pigmented cephalic tentacles may have a photosensory role in addition

Table 4

Chi-Square test results for shadow responses of snails in experimental treatments and positions.

Light intensity (lux)	Crawling		Sole of foot		Metapodium	
	$\chi^{2\,c}$	*P*	$\chi^{2\,c}$	*P*	$\chi^{2\,c}$	*P*
a) Ablated vs. Blind Snails[a]						
1.1	12.304	< 0.001	0.598	NS[b]	0.431	NS[b]
110	2.219	NS[b]	3.421	NS[b]	0.558	NS[b]
320	4.010	< 0.05	1.705	NS[b]	0.226	NS[b]
540	0.130	NS[b]	0.541	NS[b]	1.180	NS[b]
750	0.093	NS[b]	0.210	NS[b]	2.219	NS[b]
1400	1.408	NS[b]	0.181	NS[b]	0.429	NS[b]
b) Normal vs. Blind Snails[a]						
1.1	0.009	NS[b]	0.802	NS[b]	0.205	NS[b]
110	7.730	< 0.01	0.342	NS[b]	7.051	< 0.01
320	3.209	NS[b]	5.283	< 0.025	2.967	NS[b]
540	1.846	NS[b]	3.760	NS[b]	0.351	NS[b]
750	1.772	NS[b]	10.445	< 0.005	1.890	NS[b]
1400	1.315	NS[b]	12.729	< 0.001	0.039	NS[b]
c) Normal vs. Ablated Snails[a]						
1.1	15.389	< 0.001	0.002	NS[b]	0.102	NS[b]
110	13.748	< 0.001	0.943	< 0.005	6.864	< 0.01
320	0.151	NS[b]	0.612	NS[b]	10.073	< 0.005
540	2.398	NS[b]	0.989	NS[b]	6.234	< 0.025
750	1.897	NS[b]	14.375	< 0.001	3.300	NS[b]
1400	1.408	NS[b]	10.265	< 0.005	0.311	NS[b]

[a] N = 66 (normal snails) and N = 33 (blind or ablated snails) per light intensity.
[b] NS = non significant differences, $P > 0.05$.
[c] χ^2 (0.05, 1) = 3.84.

to their accepted chemo- and mechano-sensory functions (Charles, 1966). Thus, blind snails (with tentacles) demonstrated more shadow responses at low light levels than did ablated snails (with eyes). However, the photosensory role of the cephalic tentacles appears to be extremely specific, enhancing the snail's dermal photosensitivity only at low light levels (1.1 lux).

Although the sole of the foot in *N. picea* is devoid of dark pigmentation, snails in the "sole of foot" position did show some responsiveness to shadow, suggesting the presence of photoreceptors not associated with pigment granules. Similar structures, called "phaosomes" (Haszprunar, 1996), are well known in annelids (Rhodes, 1991; Jamieson, 1992; Verger-Bocquet, 1992), bivalves (Salvini-Plawen & Mayr, 1977), and gastropods (Crisp, 1971; Kunz & Haszprunar, 1992). It is also possible, that photoreception in *N. picea* is not totally confined to specialized photosensitive structures or receptors. For example, some cnidarians which lack specialized photoreceptors are photosensitive (Passano & McCullough, 1962; Mackie & Boag, 1963; Mackie, 1975), and brain neurons can act as photoreceptors and may even possibly control the diurnal rhythm of locomotion in *Aplysia* (Land, 1984).

The results presented suggest two important functions that dermal photosensitivity fulfills. First, in conjunction with the skoto-tactic responses, snails exhibit (LMG, unpublished observations), dermal photosensitivity which would appear to allow *N. picea* to mediate all phototactic responses and ensure that the snails optimize their location in their preferred habitat. Second, because *N. picea* lives in habitats that vary little in temperature, but can be cloudy for extended periods, it is evolutionarily advantageous for the species to possess an acute photosensitive mechanism that immediately alarms them of any changes in illumination caused by potential moving predators even at low light intensities. Present research is directed toward determining the relative importance of each component of the integrated photosensitive system that *N. picea* appears to use.

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